

## PLANT MORPHOLOGY AND ANATOMY IN THE TROPICS— THE NEED FOR INTEGRATED APPROACHES

P. B. TOMLINSON<sup>1</sup>

Plant morphology, like justice, must not only be done, it must be seen to be done. It must be done because it is foundational to many major disciplines—systematics, ecology, and plant physiology. Similarly plant morphology is initially an observational discipline; the pun is intentional because I want to speak from the point of view of the research worker who needs direct access to his material and the opportunity to “see” the functional significance of form and structure which is investigated.

Modern high speed travel has made easy the traditional process of what may be called “body-snatching,” i.e., the initial collection of fluid-preserved or dried materials which the plant morphologist uses for much of his work. Body-snatching has contributed the largest part to our understanding of tropical plants and needs to be actively encouraged because it provides the initial comparative background to any biological enquiry. Here I want to emphasize the need for elaboration of or departure from this classical approach in what I will call integrated studies of biological features of tropical plants. Integration here has a dual meaning, it refers to the need to combine elements of disparate disciplines— anatomy, physiology, biochemistry, ecology, and plant-animal interactions—but also emphasizes an approach which recognizes the organism itself as an integrated entity so that something of its total biology is revealed.

*Corypha* provides a simple but dramatic example of a tropical plant consisting of a single hapaxanthic module in which the switch from vegetative to sexual growth is complete, with marked contrast between the massive unbranched vegetative axis to the highly branched determinate inflorescence, with resulting proliferation of another generation of meristems. Here vegetative and reproductive phases are sharply segregated, but they must occur in the right sequence and at the right time. A striking example, which illustrates the way in which a branched organism can function as an integrated physiological unit is provided by *Cerberiopsis candelabrum* (Apocynaceae), a small tree in New Caledonia which is monocarpic (Veillon, 1971). Here a tree that is architecturally precisely branched in the initial vegetative stage eventually shows synchronous flowering and fruiting which ends in its death—rather like many annual weeds. A second species, *C. comptonii*, a treelet with smaller leaves, is not monocarpic. This genus therefore provides material for the study of a biological problem which may be approached comparatively but requires access to field populations. The plants under consideration are large and can only be represented in herbaria by fragments. An appreciation of the adaptive significance of this life style would draw on several disciplines— anatomy, physiology, and reproductive biology.

It has to be appreciated that modern travel in the tropics is easy and a

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<sup>1</sup> Harvard University, Harvard Forest, Petersham, Massachusetts 01366.

relatively inexpensive research item, compared with the many requirements of modern scientific investigation such as equipment, chemical analysis, technical support, and storage facilities. Also, common organisms which are easily accessible need prime consideration, there is no initial need for expeditions to remote areas. We are not looking here necessarily for new approaches; great scope is provided simply by the enormous diversity of tropical plants. The greatest emphasis needs to be given to the study of the morphology and anatomy of woody plants since trees dominate many tropical ecosystems with great floristic richness. This diversity is readily documented and quantified (e.g., Poore, 1968; Ashton, 1969; Rollet, 1974; Hallé et al., 1978). Here I attempt to demonstrate by means of a few selected examples the ways in which the scope of classical plant morphology and anatomy can be broadened by emphasizing functional relations, integrating the approaches of specialists in several fields, and adopting a holistic view of the plant. The object is to illustrate examples which in turn can provide guidelines.

#### PRIMARY MERISTEMS

From the point of view of the population biologist the "individual" in a tropical forest may or may not be easily recognizable for demographic purposes since clonal propagation of plants makes possible a distinction between "ramet" and "genet," to use the terms of Harper & White (1974). A useful starting point for the morphologist is to consider primary meristems as the unit making up the forest, following the suggestion of Oldeman (1974). It then becomes possible to study the ways in which primary meristems originate, function, are protected, interact with each other, and eventually die, adding a time scale and dynamic considerations to classical plant morphology. Of course, this approach is only one of many which could be adopted, but it seems of fundamental biological significance.

In this approach one can make the useful distinction between seed-originating meristems (i.e., via sexual reproduction) and vegetative meristems (both of which may be either latent or active). The production of seed-originated meristems centers on floral biology, itself an integrated discipline which will be mentioned later. Activated seed meristems are found in germinating seeds and the subject is resplendent with morphological detail (e.g., Burger, 1972; Duke, 1969; Ng, 1975, 1978) which now requires an extension into functional analysis. Ecology, physiology (e.g. of dormancy), population biology, and morphology are all interdependent at this critical phase, and yet there are few studies which attempt a functional explanation of seedling characters. Jackson (1974), to some extent, succeeded in his recognition of cryptogeal germination because he added field observations to his morphological data. The classical distinction between hypogeal and epigeal germination (or cryptocotylar and phanerocotylar, dependent on semantic tastes; Duke (1969)—which Ng (1978) has shown to be too simplistic to accommodate tropical diversity—presents in itself two contrasted biological life styles still awaiting exploration, and shows interesting analogies with contrasted branching processes (prolepsis and syllepsis), as pointed out by Hallé et al. (1978).

## BRANCHING

The vegetative meristems are of prime concern to the plant morphologist since they originate the structures in which he is interested. For active primary meristems, interaction between them within the individual tree have been outlined by Hallé & Oldeman (1970) who have provided a conceptual framework which now makes it possible to talk about tree form in a comprehensible way. This foundation can be built upon by the morphologist. An important developmental approach is to study ways in which vegetative meristems multiply, as in the study of branching patterns. The element of discovery which is still possible in descriptive tropical plant morphology is illustrated by the recent demonstration of equal dichotomy of vegetative apical meristems in a number of angiosperms (e.g., Boke, 1976; Fisher, 1976, Tomlinson, 1971; Tomlinson & Posluszny, 1977). That this is not a factor of any direct evolutionary significance is easily argued, especially with recent methods of mathematical analysis of branching patterns to provide a much needed background of quantification and theory (especially Oohata & Shidei, 1971). Equal dichotomy permits only a minimal value for a bifurcation ratio, whereas high bifurcation ratios seem adaptive in many ecological circumstances (Whitney, 1976). It seems reasonable to assume that the early development of highly controlled *axillary* branching in vascular plants has made possible the elaborated vegetative body of modern angiospermous trees (and, of course, other life forms), a statement which is little more than axiomatic (Tomlinson, 1978). A mathematical analysis of branch form provides a useful conceptual framework. It is still interesting that gymnosperms appear to lack any mechanism for generating shoots with distichous phyllotaxis and so have lost one degree of freedom much exploited by the angiosperms in their branch architecture, especially the plagiotropic shoots of many monocotyledons.

Axis differentiation in woody plants, which is a major parameter of Hallé and Oldeman's system, in the most specialized situation has a simple morphological basis since shoots with contrasted orientation can have different phyllotaxis—spiral in orthotropic, distichous in plagiotropic. The ability of the same genotype to support such contrasted primary meristems which operate contemporaneously provides scope for extended morphogenetic analysis. A comparable example is found in shoots with phase change from one type of orientation to the other during the activity of a single meristem. The best examples are provided by rhizomatous herbs where foliar dimorphism associated with sympodial growth is common, as in many Zingiberales.

Syllepsis, as contrasted with prolepsis (using these terms in the expanded definition given by Tomlinson & Gill, 1973) provides the most convincing demonstration of how limiting of elementary concepts temperate-based botany may be, since syllepsis (development of a lateral axis contemporaneous with its parent) is common only in tropical woody plants and is little developed in north temperate woody plants because lateral axes here usually undergo a period of dormancy before extension (i.e., show prolepsis). And yet these terms are needed to describe two fundamentally contrasted conditions. Why syllepsis should be so characteristic of tropical trees still awaits an ecological explanation, but recog-

nition of this simple developmental distinction opens up numerous opportunities for comparative anatomy.

The combination of anatomy and translocation physiology which integrates this dynamic aspect of shoot morphology is likely to be found in the recent demonstration by Zimmermann (1978a, 1978b) of the unequal distribution of hydraulic conductivities in trees. In particular, there are pronounced constrictions at every branch-trunk junction. This must have an anatomical basis and perhaps even provide a causal explanation for continued apical control of one type of shoot over another. Since prolepsis and syllepsis may determine differences in axis orientation in many trees, there is the possibility of analyzing continuity between dynamic morphology and subsequent function in a novel way. The anatomy of branch insertion may thus become as important in understanding the ecological significance of form in woody plants, as has comparative study of the stem-node-leaf continuum provided material for systematic and evolutionary analysis (Howard, 1974).

Secondary changes in axis orientation depending on differences in vigor that suggest hormonal mechanisms of control are important in a number of tropical trees (Koriba's model). Reaction anatomy as a functional mechanism in the organization of woody plants remains little explored, but is a topic likely to be a rich source of information in the future (cf. Fisher, 1978; Tomlinson, 1978).

#### BUD BIOLOGY

The persistence or otherwise of vegetative meristems in plants depends not only on genetic organization but also, as determined by ecological accident, on the efficiency with which shoots and their associated primordia are protected, as from predators, drought, or excess heat. Devices which can be interpreted as protective are often mechanical and conspicuous, but biochemical devices are probably equally if not more common. Here developmental anatomy, morphology, and organic chemistry need to be integrated. For larger shoots, size alone, combined with the rigidity of mature appendages, may be sufficient, as in woody monocotyledons. Many palms have efficient supplementary organs, like spines and mechanical leaf bases, as befits plants which are vulnerable because they may possess a single apical meristem incapable of vegetative branching (Uhl & Moore, 1973; Tomlinson, 1962). *Pandanus* is typically protected by serrated leaf margins. The morphological diversity of buds in dicotyledonous woody plants is well known since they so often offer useful diagnostic field characters, but the only extensive summary refers largely to temperate species (Lubbock, 1899). Although the mechanical efficiency of enveloping stipules, leaf bases, and petioles is very evident, this alone does not explain why buds seem often to be the last organs to be attacked by insect predators—or why buds can survive in the absence of mechanical sheaths. The "biology of buds" is a little explored field where the morphologist will need the assistance of biochemists in order to make progress, I believe. The concept of plant apparency (Feeny, 1976) has to be put in a morphological context, with the relative vulnerability of different parts contrasted.

In making very general surveys of tropical plants one can, for example, dis-

tinguish “wet” buds from “dry” buds, the former characterized by some fluid or resinous secretion. Wet buds commonly are associated with stipular devices which support colleters or equivalent glands, as in Rubiaceae, Rhizophoraceae, and Polygonaceae. Here the stipule may simply provide the cavity which accommodates the fluid secretion. Even where the stipules are small (“vestigial” to some comparative anatomists), as in many Euphorbiaceae, Ulmaceae, Celastraceae, and Elaeocarpaceae, they are likely to perform a vital function, since they can mature before associated leaf primordia, and their biochemical specialization may be indicated by their high tannin content, an observable microscopic feature. In other buds which lack stipules there is no such division of labor, and the leaf primordia themselves are tanniniferous. Secretions which dry as conspicuous, resinous or varnishlike coatings of unknown chemical composition, but probably polysaccharides, are common in tropical woody plants—they may make the bud distasteful, resistant to drying, reflect damaging wavelengths, and mechanically impede chewing insects. This exuded material is something that production ecologists should not overlook, since it is often exfoliated in considerable quantities. In *Ceriops* (Rhizophoraceae) between 25 and 40% of the dry weight of the bud is made up of this varnish. Initially it simply fills the quite considerable free space between stipules and leaf primordia—at this stage it is a close packing device which is related to the periodicity of growth extension; subsequently the varnish becomes a casing to the expanding leaves and internodes, with unknown biological properties; finally it sloughs off. The material has not yet been analyzed biochemically, but a large amount is produced and lost each time a leaf pair expands.

A possible biological function for bud secretions in other Rhizophoraceae has been shown recently by Richard Primack, in Queensland. He found that a galactose-rich exudation served as a bird-attracting device in *Rhizophora stylosa*, since nectar-feeding birds would lick this sweet fluid which is apparently produced by the nonvasculated stipular glands (colleters). Such birds are likely to also pick off insects, this grooming being of presumed benefit to *Rhizophora*. Here, therefore, initial studies on the anatomy of colleters have an extension into biochemistry and plant-animal interactions.

The term “naked bud,” which is sometimes used to describe meristems without specialized mechanical protection, is not particularly appropriate because leaf primordia at an arrested state of development are frequently associated with a specialized but ephemeral indumentum, or with latexlike secretions. The initial need is not for elaborate categorization, but for the examination of specific case histories with the concept of the bud as a biological unit given prime consideration.

Emphasis must be given to the construction of buds in relation to the method of shoot extension, i.e., whether rhythmic, continuous, or intermittent (without regular periodicity). In many tropical woody plants a stipular organ can serve as an “instant” bud scale, the shoot ceasing to extend without reference to any endogenous rhythm but still retaining a protective cap. The relation between stipule position and the region of extension is of interest. In most examples internodal extension occurs beyond the level of stipule insertion, but in some

Cunoniaceae, a family characterized by well-developed interpetiolar stipules, the stipule pair is carried up with the bud by extension of the internode below it. The idea that bud morphology is a dynamic and not a passive subject is one that can be encouraged by the comparative study of the wide diversity of plants available in the tropics.

Internal secretions, most noticeable in those numerous tropical families with latex, often of commercial importance (Apocynaceae, Asclepiadaceae, Moraceae, Sapotaceae, and Euphorbiaceae) provide an area for integrated studies combining anatomy, developmental morphology, chemistry, and adaptive biology. This can be illustrated in a spectacular way by the recent report that the New Caledonian endemic *Sebertia acuminata* (Sapotaceae) accumulates as much as 25% by dry weight of the heavy metal nickel in its latex (Jaffré et al., 1976). This is undoubtedly an exceptional case, but it does indicate part of the mechanism whereby a plant can tolerate soils with a high content of heavy metals and shows an interesting correlation between plant anatomy and mineral nutrition. Both the distribution of laticifers within this plant, and the distribution of heavy metals and inorganic compounds in laticiferous organisms offer themselves as subjects for study. It is known that nickel accumulators are not necessarily laticiferous (Brooks et al., 1974), but where does nickel accumulate in plants of high nickel content? Electron microprobe analysis of appropriate organisms could usefully integrate ecology, anatomy, and chemistry. Of interest is the way in which herbarium specimens have been used in this research (Brooks et al., 1977) showing the lasting value of "snatched bodies."

#### FLORAL BIOLOGY

This area represents perhaps the most profitable one for integrative studies, and a number of recent workers have combined comparative and developmental anatomy with field study of flower visitors and pollination biology. In part this is a response to Carlquist's (1969) critique of the general subject of floral anatomy, but much reflects the increasing field orientation of modern morphologists. The most extended study of this kind is that of Uhl & Moore (1977) on palms in which a syndrome of characters is described in detail for inflorescence and flower patterns in six examples representing two anemophilous and four different entomophilous modes of pollination. This study has as its basis one of the most complete systematic and anatomical backgrounds known for any family of tropical plants (Moore, 1973) and should serve as a model for future studies. It extends the concept of "protection" of meristems to ovules and pollen, but backward in time to the vegetative meristems which ultimately produce them, via the often elaborate inflorescence to the floral envelopes and mechanisms which assist in fertilization and then anticipates the later processes which contribute to the formation of seeds and fruits. We therefore add a time scale and additional biological dimensions to comparative studies which began with studies of floral vasculature.

Reproduction "strategy" may even have to be integrated with photosynthetic "strategy" since position of flowers or inflorescences can determine the architectural model in Hallé and Oldeman's system. Of interest are those contrasted

examples where the presence of terminal versus lateral inflorescences, resulting in determinate or indeterminate axes, in turn produces an architecture which is the morphological analogue of monolayer and multilayer, to use the terminology of Horn (1971) for probable contrasted photosynthetic strategies in trees. This kind of example shows how emphasis of a particular dynamic aspect of one phase in the life cycle of a plant inevitably leads from one topic to another, such is the nature of an organism as an integrated whole.

A field-orientated approach to comparative morphology which illuminates floral structure is shown by recent studies on the mangrove Rhizophoraceae (Tomlinson et al., in preparation). This involves 4 genera and about 20 species with a comparable vegetative morphology (architecture, bud morphology) and habit (marine swamps) but with evident niche diversification shown by quite complex ecological zonation, which is reflected morphologically in diversity of aerial root development. A common floral plan is involved, indicative of a common evolutionary ancestry but with immediately obvious variation in such features as inflorescence branching, flower size, orientation, and number of parts. A dominant feature is the dehiscence of stamens within the unopened flower. Functionally at least 6 types of floral mechanism can be recognized according to the way parts behave in relation to pollen vectors. These types transcend taxonomic boundaries because a single genus can include contrasted mechanisms (*Ceriops*) or be adapted to different visitors (*Bruguiera*). An unusual mechanism which is the result of considerable developmental complexity is a catapult release of pollen, with stamens initially enclosed by petals in a spring device triggered by a flower visitor. Despite this common piece of engineering, flowers are visited more or less exclusively by birds on the one hand, insects on the other, with further specialization according to the type of insect—moth versus butterfly, for example.

Extending these observations in a comparative way, considerable circumstantial evidence accrues that the genus *Rhizophora* is an exceptional component of mangrove communities because it is wind pollinated. This may be one reason for its evident ecological success and is the basis for an understanding of genetic aspects of its species interrelationships which are suggested by certain taxonomic peculiarities in the genus. This step-by-step development of our understanding of this widespread and important genus began with simple curiosity about its morphology and anatomy. The essential ingredients in the success of this continuing research have been repeated access to natural populations and collaborative work with other specialists—field ecologists, population biologists, and biochemists and attempts to understand different components in a biological continuum.

#### CONCLUSIONS

The examples chosen are few and refer to a restricted field. Similar approaches to different topics could have been adopted. Instead of primary meristems, the secondary meristems of tropical woody plants could have provided a focal point. Knowledge of fluctuations in the activity of vascular cambia in tropical trees is very scant and we largely lack the important ecological param-

eter this provides in temperate trees—the ability of an observer to determine tree age quite accurately is missing in tropical forests.

The structure and development of root systems in tropical plants is little explored, especially the interaction between roots and soil microorganisms (cf. Janos, 1975). For this topic, even descriptive morphology is at a very elementary stage.

One particularly useful field which needs expanding is the study of the morphology and anatomy of tropical crop plants since a knowledge of their response to pathogens and pests depends on a knowledge of their normal structure. However, there are no detailed and comprehensive accounts of the structure of major tropical crop plants like coconut, oil-palm, coffee, cocoa, rubber, and so on. A particular deficiency is in studies of development morphology. The integrated activities of a diversity of workers is required here.

The conclusion then is that plant anatomy and morphology remains a central field of tropical inquiry, but not as an isolated or static discipline. The morphologist has to combine his specialized abilities with those of colleagues in other fields. Once this elementary principle is accepted we can move on to the more important task—devising the most efficient means to apply this principle.

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